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An Analysis of the Orientation of 'Magnetic' Termite Mounds

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Abstract

North–south pointing tendency is very strongly developed in mounds of a 'magnetic' termite, *Amitermes laurensis*, in northern Australia. Determination of orientation in 248 termitaria in Arnhem Land showed a total range from 349° to 030° (true). Angular means from each of four separate study sites were 007°39′ (n = 47), 010°35′ (n = 101), 006°56′ (n = 50) and 008°34′ (n = 50). Orientation of mounds built among trees of savannah woodland is not less accurate than that of mounds built on open plains.

The shape of mounds in plan view is variable. They may be symmetrical, or show concavity of either eastern or western face. Shape–frequency distributions for each locality were heterogeneous, even between localities in close proximity. It is suggested that mound shape may be determined genetically rather than by environmental factors.

Introduction

The large wedge-shaped nests of so-called 'magnetic' or 'compass' termites have excited interest and speculation for many years because of the orientation of their elongated axis in a north–south direction. Many authors have referred to this orientation, notably Jack (1897), Mjöberg (1920, in Hill 1942), Hill (1942), Serventy (1967), Gay and Calaby (1970), and Grigg (1973). Most of the earlier literature is devoted to speculation about the biological significance of north–south orientation. Grigg (1973) showed that north–south orientation provides a more benign thermal environment for the termites living in the mounds, compared to that of a mound in experimental east–west orientation. He suggested that the elongated wedge-shaped mound may have evolved to maximize the surface area : mass ratio, and thus to facilitate gas exchange across the walls of the nest. Thermal considerations then predicate north–south orientation of the elongated mound.

The main aims of this study were to determine: (1) the mean angular direction of the mounds; (2) the accuracy of orientation; precise information which has not been documented previously.

Another aim was to compare the accuracy of orientation in open and semi-shaded fields. Grigg (1973) has shown that the presentation of a broad face of the mound to the sun, both early and late in the day, combined with presentation of the mound's narrowest profile to the midday sun, ensure high and relatively stable core temperatures during the day. Where mounds occur among trees and are shaded for substantial periods each day, strict north–south orientation may not necessarily provide the best thermal conditions inside the mound.

There will be larger differences in the amount, direction and timing of receipt of solar radiation among mounds built among trees (Fig. 1) than among mounds built on open plains (Figs 2–4). It seems reasonable to propose, therefore, that orientation of mounds may be more variable in savannah woodland than in open plains.

In addition, some observations on the shapes of these interesting structures are analysed and discussed.

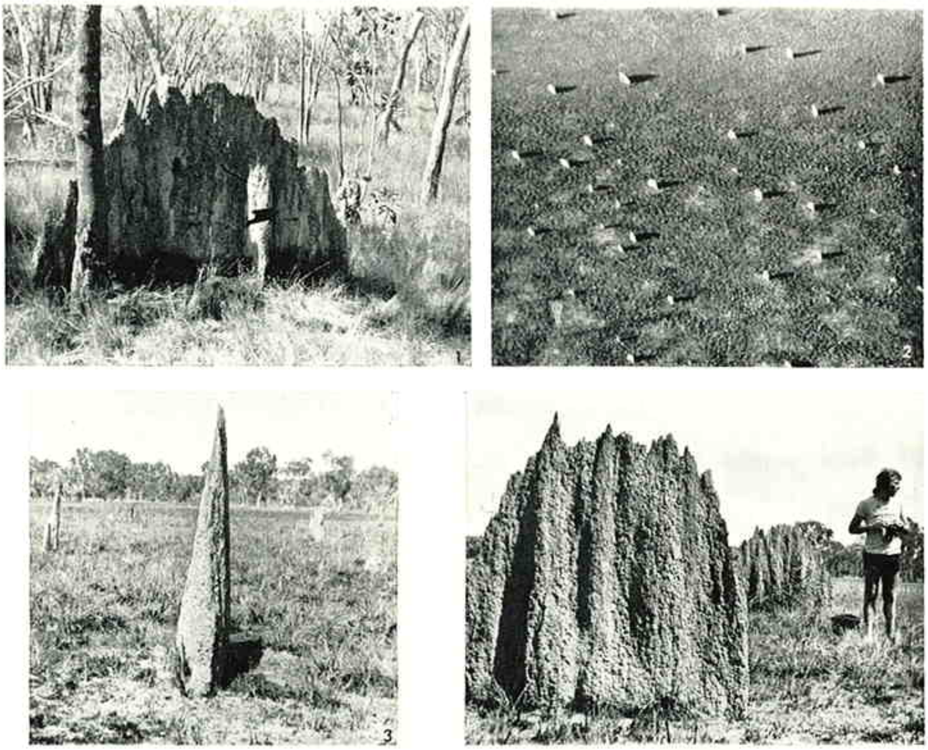

Fig. 1. Termitarium in a semi-shaded locality on Gudjerama Creek, N.T.

Fig. 2. Aerial view of magnetic termite mounds near the Tomkinson River, N.T.

Fig. 3. A magnetic mound from the north.

Fig. 4. The same mound from the east.

(For scale, termitaria in the study area average 1·5–2·0 m in height.)

Methods

'Magnetic' termitaria are constructed by three closely related species of tropical Australian termites. *Amitermes meridionalis* (Froggatt) always builds meridional mounds, but *A. laurensis* Mjöberg and *A. vitiosus* Hill build them only in some circumstances, particularly in low-lying, ill-drained areas (Gay and Calaby 1970). Mounds of *A. laurensis* were investigated in this study.

Field Work

The study was carried out near Maningrida, 320 km east of Darwin, N.T. (Fig. 5). Magnetic termitaria were located in a semi-shaded situation on Gudjerama Creek at the crossing of the Maningrida–Cadell road. This site was designated field I. Unshaded fields of magnetic termitaria were known to occur in many places along the eastern bank of the Tomkinson River, so a low-level aerial survey was made to select fields which were close to the river and with abundant mounds.

Three sites were chosen, designated II, III and IV (Fig. 5), all of unshaded (or 'open') type, which could be reached by speedboat from Maningrida.

The orientation of each mound was determined with a prismatic compass by an investigator standing some 4–5 m south of a mound and in line with the axis of elongation. This was particularly easy to determine in mounds whose ground plan was symmetrical (Fig. 6*a*). Many nests, however,

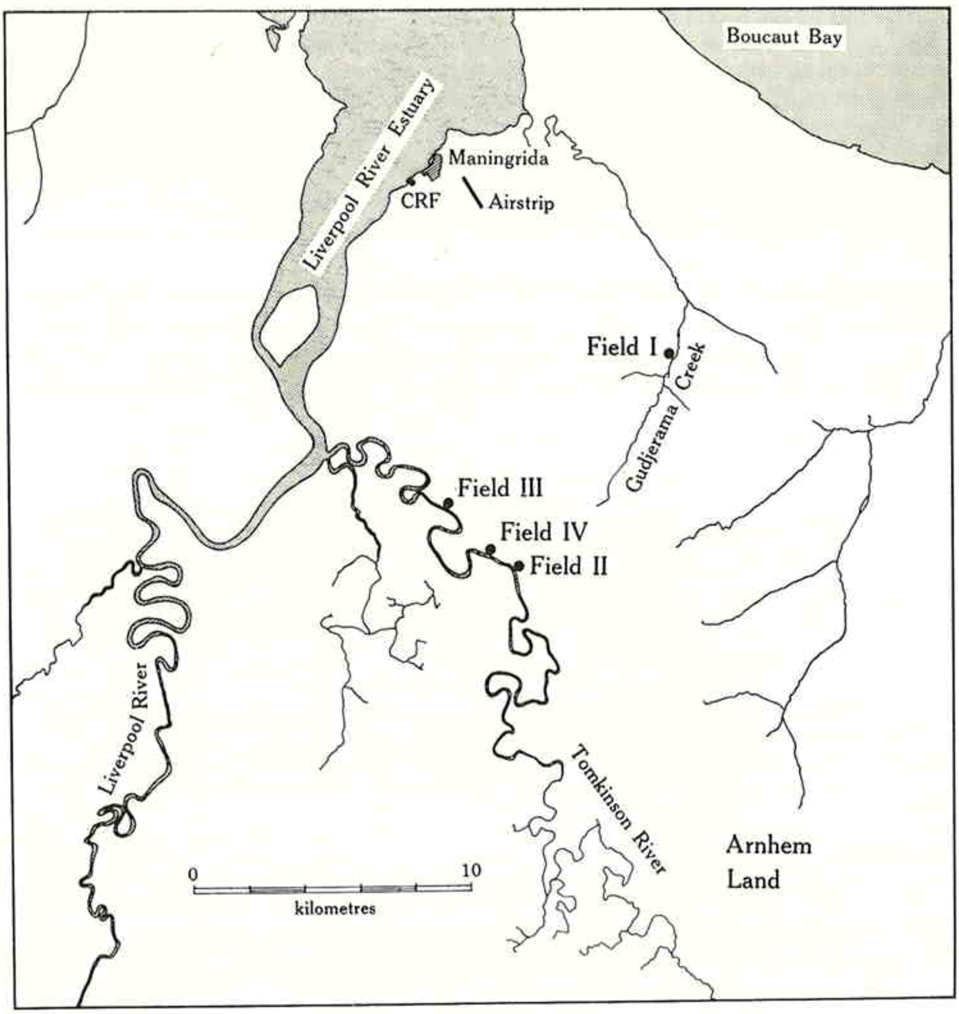

Fig. 5. Map showing location of the four study sites. CRF, Crocodile Research Facility.

are concave towards either the east or the west. In such nests the axis of elongation was defined as indicated by the dotted line in Figs 6*b*, 6*c*. This definition can be justified because a nest seems to grow symmetrically at both ends, so that the axis of elongation maintains the same (or very similar) orientation during growth. Some mounds were irregular in plan view (Fig. 6*d*) and their axis of elongation was determined subjectively. Despite the variability in nest shape and a certain degree of subjectivity in deciding the axis of elongation, agreement between repeated measurements of a series of mounds on different occasions was within one degree. All measurements were made by the same person (G.C.G.). Magnetic bearings were converted to bearings relative to true north by adding 4°, the local magnetic variation according to the appropriate current World Aeronautical Chart.

Details of concavity of a mound to east or west were also recorded, as well as any major irregularities of nest shape.

Statistical Analyses

Angular distributions are not satisfactorily analysed by linear normal statistics. Because of the regular periodicity of the circle, such data are more appropriately analysed by statistics based on the von Mises (circular normal) distribution (Batschelet 1965; Mardia 1972). This distribution is characterized by two parameters, $\bar{x}_0$ (the angular mean, or 'preferred' direction) and $\hat{K}$ (the concentration parameter). These parameters are wholly analogous to the mean and variance of the linear normal frequency distribution. The concentration parameter, $\hat{K}$, is directly related to the mean resultant vector, $\bar{R}$, which can be estimated from samples of the population (see Batschelet 1965). Full accounts of appropriate tests of null hypotheses concerning angular means and concentration parameters can be found in Batschelet (1965) and Mardia (1972). All angles measured in this study were in the range 0–π radians (180°) and analyses were performed on doubled angles to transform them to a von Mises distribution with appropriate corrections (Mardia 1972).

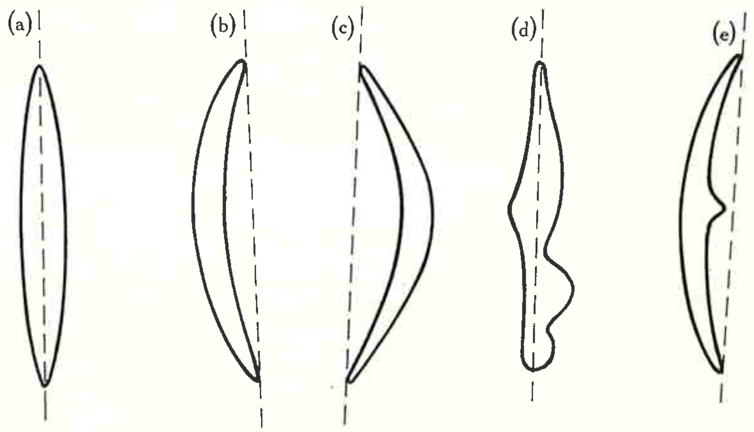

Fig. 6. Stylized plans of differently shaped mounds. Dotted lines indicate how orientation was defined.

Results

Orientation

The angular orientation of 248 mounds was measured: 47 from field I, 101 from II, 50 from III and 50 from field IV. Measurements confirmed the casual observation that there is moderate variability in the orientation of mounds. A histogram plot of results from each field is shown in Figs 7*a*–7*d*, and the combined data from all four fields in Fig. 7*e*. The overall range was from 349° to 030° (true).

(i) *Accuracy of orientation in open* v. *semi-shaded fields*

Accuracy of orientation was tested by a multiple comparison of the concentration parameters for the sample from each field. The resultant mean vector ($\bar{R}$) of the pooled sample was greater than 0·70, so untransformed data could be analysed by Bartlett's test for homogeneity of concentration parameters (Mardia 1972).

There were no significant differences between the concentration parameters of the four samples ($\chi^2 = 0{\cdot}31$; 3 d.f.; $P > 0{\cdot}05$). Thus, the orientation of mounds with respect to their angular means is equally variable in the four fields.

(ii) *Comparison of angular means*

The angular mean, with 95% confidence limit, of the sample from each field is as follows:

Field I (n = 47)	007°39′±1°	Field III (n = 50)	006°51′±1°
Field II (n = 101)	010°35′±1°	Field IV (n = 50)	008°34′±1°

As there was no heterogeneity of concentration parameters, and because the mean resultant vector of the pooled data was greater than 0·70, the angular mean orientations of mounds in the four fields could be tested by analysis of variance (Mardia 1972). The analysis of variance showed significant differences between samples ($F = 2{\cdot}71$; $0{\cdot}025 < P < 0{\cdot}05$). There is no obvious testing procedure for multiple comparisons of four samples, but construction of (angular) confidence limits around the angular means of each sample showed that the means of fields I and IV fall within the 95% confidence limits of fields III and I respectively. This indicates that mean orientation in each of these three fields was not significantly different (see tabulation above). Further, the mean orientation of mounds in field II fell outside the 99% confidence limit of the angular mean of the pooled samples from fields I, III and IV. This implies that the mean orientation of mounds in field II is significantly different from that in the other three fields.

Table 1. Frequency distribution of different shapes (in plan view) of mounds in fields I–IV

Field No.	Not concave	Concave east	Concave west	Total
I	0	0	47	47
II	69	19	13	101
III	21	9	20	50
IV	38	10	2	50
Total	128	38	82	248

Shape

The only aspect of shape which was analysed was the relative frequency of concave east, concave west, or symmetrical (not concave) mounds. Possible associations between angular orientation and shape, and between angular orientation and geographic location (field) were investigated.

(i) *Angular orientation and shape*

Mounds from field II were not considered in this analysis because the earlier analysis showed them to have a different mean orientation from those in the other fields. As before, untransformed data could be analysed for homogeneity of concentration parameters by Bartlett's test. No significant heterogeneity was found among the variabilities of orientation of the three shapes ($\chi^2 = 0{\cdot}23$; $P > 0{\cdot}75$). Lack of heterogeneity between samples allowed analysis of variance of angular means of the three samples. There were no significant differences between the three samples ($F = 2{\cdot}13$; $0{\cdot}25 > P > 0{\cdot}05$). There is, therefore, no apparent difference in mean orientation as a result of the shape of the mounds.

(ii) *Geographic location and shape*

Visual inspection of the data (Table 1), suggested that the frequency of occurrence of each of the three shapes of mounds is different in different fields. This was confirmed by χ^2 analysis ($\chi^2 = 135 \cdot 25$; 6 d.f.; $P < 0 \cdot 001$). The high frequency in field I of mounds concave to the west contributes strongly to this result. Re-analysis of the data from fields II, III and IV gives $\chi^2 = 26 \cdot 28$ (4 d.f.; $P < 0 \cdot 001$). Thus, even fields in close proximity may show significant differences in their shape–frequency distribution.

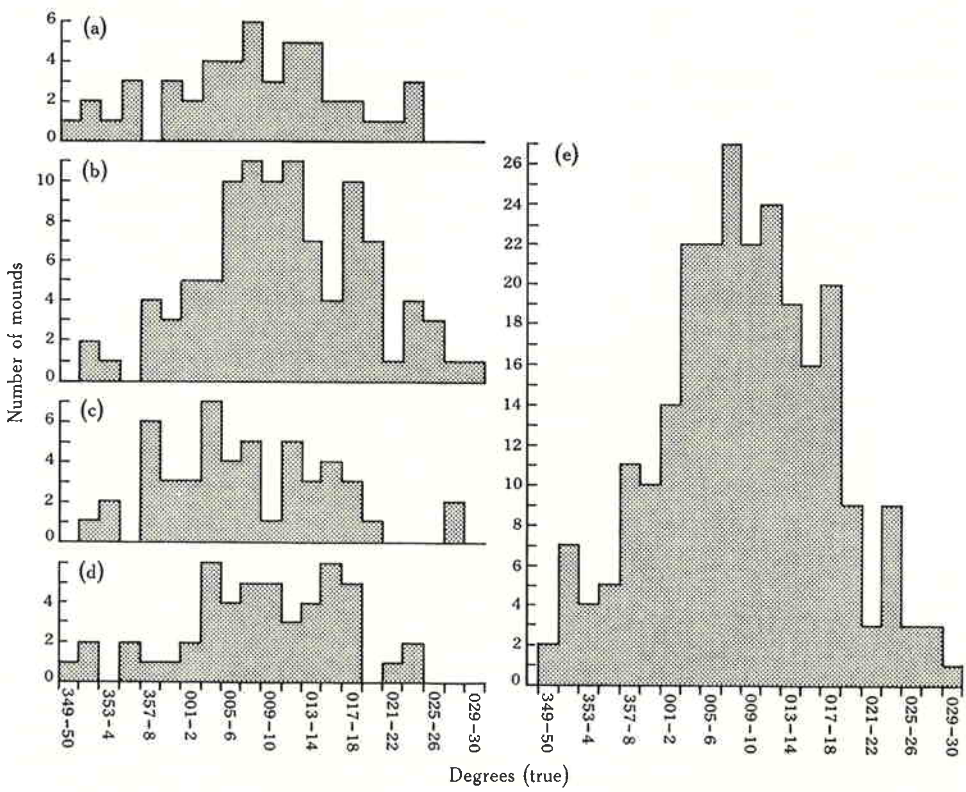

Fig. 7. Histograms showing the variability of orientation of termitaria in fields I–IV (*a–d*) and in all fields combined (*e*). (Even though the mean angle in field II differs from that in the other fields, its data are included in (*e*) in order to show the total extent of variability.)

Discussion

Mean Direction

Even with field II included it is clear that the north–south pointing tendency is very strongly developed. No ready explanations are available for the angular mean orientation (approximately 8°) being significantly different from true and magnetic north, nor the unexpected difference of orientation in field II. Clearly, the cues for orientation remain unknown.

Accuracy of Orientation

Since there is no direct equivalent of standard deviation or variance among statistics derived from angular normal distributions, we can give no familiar value to express the spread of the data. Visual representation is given in Fig. 7. Lack of significant differences between concentration parameters suggests very strongly that orientation in field I (semi-shaded) is not less accurate than in the open fields.

There is, therefore, no evidence to suggest that construction of the mound is modified in response to periods of shading at the site. The environmental cues by which orientation is established are not known, but it is clear that a response to either thermal gradients or to ambient solar radiation cannot be assumed to be the major factor.

Shape; some Speculations

The heterogeneity of shape–frequency distribution, even between fields in close proximity, is interesting. One might suppose that the shape either depends upon responses to environmental factors (e.g. moisture, slope, etc.) or is genetically determined.

It would be difficult to support an hypothesis based on control by environmental factors, for in fields II, III and IV all three shapes are present in close proximity to each other and in similar habitats. A genetic argument may, however, be easier to sustain. Because the worker termites derive from a single mated pair of alates, or supplementary queens derived therefrom, the eventual shape of the mound, if genetically determined, is an expression of the possible combinations of parental genotypes only. In view of the correlation discussed above, and the low dispersal ability of alates on the mating flight (Gay and Calaby 1970), it is tempting to postulate genetic rather than environmental control over whether the mound is concave east, west, or not at all. This hypothesis could explain the lack of any shapes other than concave west at field I, for this isolated field might have been colonized, by chance, by homozygous alates, with subsequent local dispersal but no further immigration. These questions must wait further investigation.

Acknowledgments

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